Wilson Bull., 105(2), 1993, pp. 301–315

PHYLOGENETIC AND BIOGEOGRAPHIC RELATIONSHIPS IN THE NEOTROPICAL GENUS *GYMNOPITHYS* (FORMICARIIDAE)

SHANNON J. HACKETT[1,2]

ABSTRACT.—Evolutionary relationships among obligate ant-following birds in the genus *Gymnopithys* were addressed using phenetic and phylogenetic analyses of allozyme characters. Genetic variation at 37 gene loci was analyzed across all four species in the genus and within two species (Bicolored Antbird [*G. leucaspis*], and White-throated Antbird [*G. salvini*]). Interspecific genetic distances were high, and comparable to other studies of Neotropical birds, which exceed those in many temperate zone species. Within the genus, Lunulated Antbird (*G. lunulata*) and *G. salvini* were sister taxa. There was only weak support for a sister-taxon relationship between *G. leucaspis* and the Rufous-throated Antbird (*G. rufigula*). Within *G. leucaspis* and *G. salvini,* high F_{st} indicated substantial genetic subdivision, again comparable to other Neotropical birds and much greater than temperate zone birds. Increased age of population isolation is proposed to account for the high genetic divergence in Neotropical birds. *Received 15 May 1992, accepted 24 Nov. 1992.*

Despite widespread interest in biogeographic patterns of Amazonian birds, few phylogenies of Neotropical birds and no analyses of the genetic structure of widespread Amazonian species have been published. In this paper, I address phylogenetic and biogeographic relationships among populations within two widespread species of *Gymnopithys* antbirds (Formicariidae) and among all four species in the genus using allozyme characters. In addition, I summarize and add to the growing body of genetic information on Neotropical forest birds.

All species in the genus *Gymnopithys* are obligate ant-following birds (Willis 1967, 1968) distributed throughout lowland forests of Central and South America (from Honduras south to Brazil). Ant-following birds obtain food by following ant swarms and feeding on insects flushed by the moving swarm (Willis 1967). Limited systematic work based on external morphology has been done on this genus; four species are currently recognized: White-throated Antbird (*G. salvini*), Lunulated Antbird (*G. lunulata*), Bicolored Antbird (*G. leucaspis*), and Rufous-throated Antbird (*G. rufigula*) (Zimmer 1937, Meyer de Schauensee 1966). The species are mostly allopatric, with rivers forming the boundaries of ranges (Fig. 1).

Compared to other vertebrates, birds have low levels of allozyme differentiation at all levels of the taxonomic hierarchy (Avise and Aquadro 1982). The generality of low avian genetic distances was challenged by

[1] Museum of Natural Science and Dept. of Zoology and Physiology, Louisiana State Univ., Baton Rouge, Louisiana 70803.
[2] Present address: Dept. Ornithology, American Museum of Natural History, Central Park West at 79th St., New York, New York 10024.

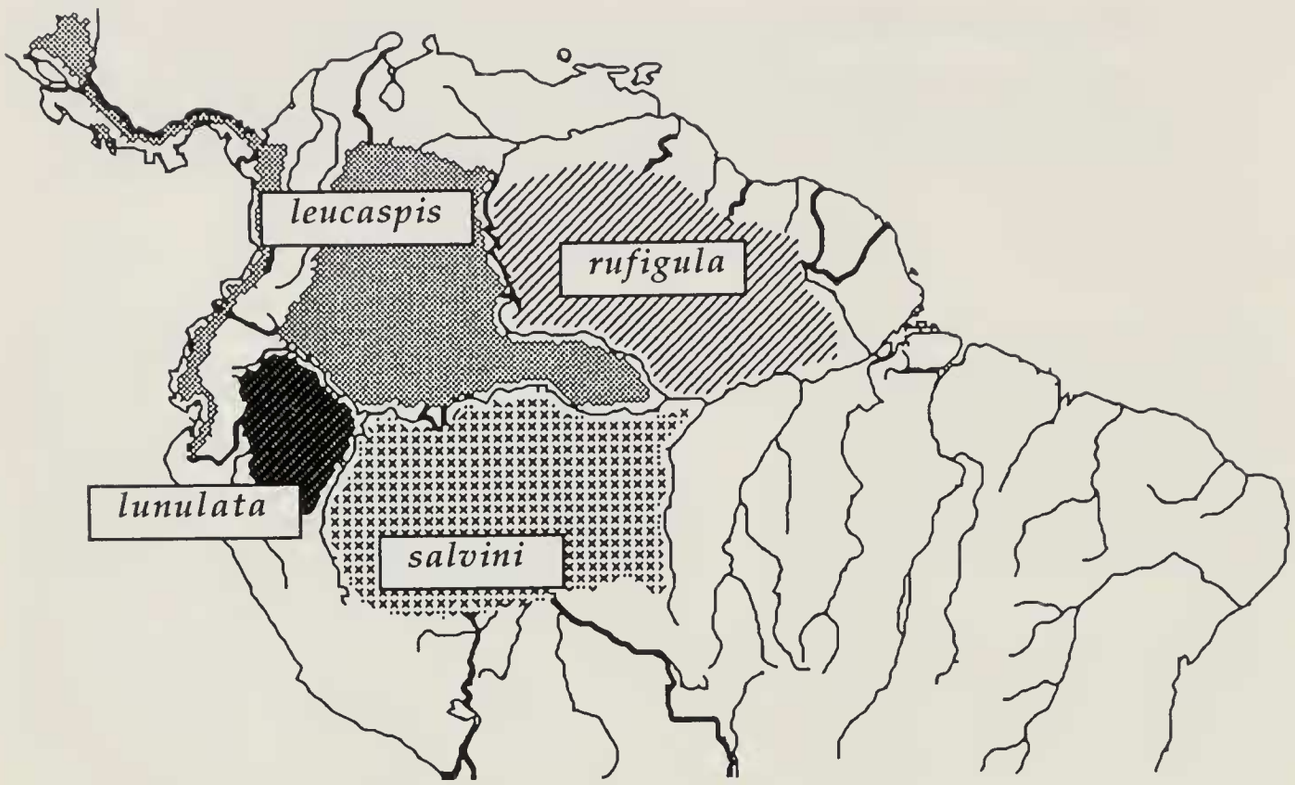

FIG. 1. Ranges of all *Gymnopithys* species.

studies of genetic differentiation in Neotropical birds (Capparella 1987, 1988; Gerwin and Zink 1989; Gill and Gerwin 1989; Hackett and Rosenberg 1990). These studies demonstrated that bird populations and species are more genetically differentiated (subdivided) in lowland tropical forests, although they still do not reach levels found in some other vertebrate groups. Hypotheses proposed to explain greater population subdivision include increased age of Neotropical taxa, low levels of gene flow between Neotropical avian demes, and differences in social systems (for example, reduced effective population sizes due to lekking behavior).

METHODS

Samples were obtained for all species of *Gymnopithys,* six population samples representing four subspecies of *G. leucaspis* and two population samples from one subspecies of *G. salvini.* Three other genera of ant-following birds, the Sooty Antbird (*Myrmeciza fortis*), White-plumed Antbird (*Pithys albifrons*), and Hairy-crested Antbird (*Rhegmatorhina melanosticta*), suggested by Willis (1967) to be closely related to *Gymnopithys,* were used as outgroups. Abbreviations for the outgroups are as follows: MFORT, PALBI, and RMELA, respectively. All tissue samples were from the Louisiana State University Museum of Natural Science Frozen Tissue Collection. Collecting sites, sample sizes, and acronyms for all taxa are listed in Table 1. Although my sample sizes are small, Gorman and Renzi (1979) demonstrated that one or few individuals per taxon provide robust estimates of genetic distance as long as the number of loci examined is reasonably high and heterozygosity is low (conditions met by this study). The conservatism of avian allozyme divergence, fixed or nearly fixed allozymes unique to certain groups of this study, and low heterozygosity may minimize the sample-size bias for estimating genetic distances predicted by Archie et al. (1989).

TABLE 1

COLLECTING LOCALITIES, ACRONYMS, AND SAMPLE SIZES (IN PARENTHESES) FOR *GYMNOPITHYS* SPECIMENS USED IN THIS ANALYSIS

Taxon	Collecting locality
Gymnopithys leucaspis bicolor (3)	Panama: Prov. Darién; NW Cana (LEUDA)
G. leucaspis olivascens (3)	Costa Rica: Prov. Puntarenas; Peninsula de Osa (LEUCR)
G. leucaspis aequatorialis (3)	Ecuador: Prov. Esmeraldas; El Placon (LEUEC)
G. leucaspis castanea (3)	Peru: Prov. Loreto; N Río Napo (LEUNN)
G. leucaspis castanea (3)	Peru: Prov. Loreto; N Río Amazonas (LEUNA)
G. leucaspis castanea (3)	Peru: Prov. Loreto; E Río Yanayacu (LEUEY)
G. rufigula (1)	Venezuela: TF Amazonas; Cerro de la Neblina (RUFIG)
G. salvini maculata (2)	Peru: Prov. Loreto; S Río Amazonas (SALSA)
G. salvini maculata (2)	Bolivia: Dpto. Pando; near Cobija (SALPA)
G. lunulata (1)	Peru: Prov. Loreto; S Río Marañon (LUNUL)

Standard horizontal starch-gel electrophoresis of proteins was performed as outlined in Hackett (1989) and Hackett and Rosenberg (1990). Each locus was scored on two buffer systems to reduce influences of hidden variation (Hackett 1989). Alleles were coded by their relative mobility from the origin; the most anodally migrating allele was coded "a." Isozymes were coded in a similar manner, with a "1" indicating the most anodally migrating isozyme. Locus acronyms follow Murphy et al. (1990).

I used the computer program BIOSYS-1 (Swofford and Selander 1981) to compute genetic distances (Rogers 1972, Nei 1978), a UPGMA phenogram, and Distance-Wagner (Farris 1972) trees using the multiple addition criterion of Swofford (1981); all trees were rooted at the non-*Gymnopithys* ant-following formicariids (*Myrmeciza fortis, Pithys albifrons,* and *Rhegmatorhina melanosticta*). The computer program PHYLIP (Felsenstein 1986) was used to construct two trees from Rogers' (1972) genetic distances: one that assumes a constant rate of evolution ("KITSCH"), and one that does not ("FITCH"). Cladistic assessment of allelic variation was performed by coding each locus as a multi-state unordered character (and alleles at each locus as character states) using the computer program PAUP 3.0L (Swofford 1990). Also, in another cladistic analysis, phylogenetically informative alleles were considered as characters and coded as present or absent (see Rogers and Cashner [1987] for defense of this method of coding; see also Mickevich and Mitter [1981], Buth [1984], and Swofford and Berlocher [1987] for problems with this method of coding). One hundred bootstrap replicates were performed on each cladistic analysis to assess confidence in the branching pattern (Felsenstein 1985, Sanderson 1989). The homoplasy excess ratio (HER) proposed by Archie (1989a, b) was calculated to give a measure of homoplasy less influenced by number of taxa than the consistency index (CI; Kluge and Farris 1969) and to assess whether the distribution of the allozyme data was nonrandom.

Measures of genetic population subdivision, F_{st} (Wright 1978), were calculated for *G. leucaspis* and *G. salvini* using a computer program provided by G. F. Barrowclough that takes into account small numbers of individuals sampled from a population.

RESULTS

Levels and patterns of genetic variation at 37 presumptive gene loci were resolved (Tables 2 and 3). Nineteen loci (51%) were variable within or among species. Average genetic distance (Nei 1978; ± SD) within *Gymnopithys* (N = 6) as a whole is 0.173 ± 0.025; within *G. leucaspis* (N = 15) genetic distances average 0.053 ± 0.012. Genetic distance averages 0.065 among the three population samples of *G. leucaspis castanea* (LEUNN, LEUNA, LEUEY). The two populations samples of *G. salvini* differ by a Nei's (1978) genetic distance of 0.028. F_{st} among the six populations of *G. leucaspis* is 0.365, and between the two *G. salvini* populations F_{st} is 0.333 (Table 4).

The UPGMA phenogram (Fig. 2) reveals that the four species of *Gymnopithys* form a group, as do the six population samples of *G. leucaspis* (representing four different subspecies). There is weak support, as evidenced by short branch lengths, for the *bicolor* group of *G. leucapsis* from Middle America and western South America (LEUEC, LEUDA, LEUCR) as genetically distinct from the Amazonian *leucaspis* (LEUNA, LEUNN, LEUEY). *Gymnopithys rufigula* is most similar to *G. leucaspis,* and *G.*

salvini and *G. lunulata* form a group. This topology is also found in the KITSCH and FITCH trees (branch lengths available from author on request). The Distance-Wagner tree differs in placing the Costa Rican sample of *G. leucaspis* (LEUCR) basal to the five other population samples. Because the four distance analyses suggested only minor differences in branching pattern, I assume that variation in rates of allozyme evolution across *Gymnopithys* species is not a significant factor influencing branching topology.

Cladistic analysis of loci with the alleles as unordered character states (not shown) resulted in 12 equally most parsimonious trees, with a consistency index (CI) of 1.0 and a homoplasy excess ratio (HER) of 0.88. These data indicate that there is little homoplasy in the data set and that the data are nonrandom; that is, there is phylogenetic information contained in the allozyme data. However, the consensus of these 12 trees resulted in little resolution. The genus *Gymnopithys* is monophyletic; the monophyly of population samples of *G. leucaspis* and *G. salvini* indicates the monophyly of each of these two species. *Gymnopithys salvini* and *G. lunulata* are sister taxa. However, the sister-taxon relationship between *G. rufigula* and *G. leucaspis* suggested in Fig. 2 is not shown here; *G. rufigula, G. leucaspis,* and *G. lunulata/G. salvini* form an unresolved trichotomy. The relationships among population samples within *G. leucaspis* are also unresolved.

The topology when alleles are coded as present or absent (Fig. 3; two most parsimonious trees, CI = 0.700, HER = 0.78) supports monophyly of both the genus *Gymnopithys* and the population samples of *G. leucaspis* and *G. salvini.* This tree differs from the distance analyses mainly in the relationships among the six population samples of *G. leucaspis.* Samples of *G. leucaspis* from eastern Panama (Darién) and Ecuador have the same alleles and are identical for this analysis (they differ in allele frequency only). Bootstrap values for the nodes (Fig. 3) indicate that there is only weak support for the sister-taxon relationship between *G. rufigula* and *G. leucaspis* suggested by the distance analysis. There is stronger support for *G. salvini* and *G. lunulata* as sister taxa.

DISCUSSION

Genetic data.—Genetic distances within the few other species of Neotropical birds studied average 0.052 (range 0.003 in *Pithys albifrons* to 0.066 *Chiroxiphia pareola*; see Hackett and Rosenberg 1990). The average within *G. leucaspis* (0.053) is comparable to the other Neotropical species, and of an order of magnitude greater than north temperate birds (0.005, Barrowclough and Corbin 1978; 0.02, Barrowclough and Johnson 1988). In addition, F_{st} values (Table 4) suggest a high degree of subdivision among

TABLE 2

ALLELIC FREQUENCIES AT 19 VARIABLE LOCI FOR TAXA ANALYZED IN THIS STUDY[a]

	LEUEC	LEUDA	LEUCR	LEUNA	LEUEY	LEUNN	SALSA	SALPA	LUNUL	RUFIG	PALBI	RMELA	MFORT
IDH1	b	b	b	b	a (0.333) b (0.667)	a	b	b	b	b	b	b	b
IDH2	c	c	c	c	c	c	c	c	a	b	c	c	c
AAT1	a	a	a	a	a	a	a	a	a	a	a	a	b
PGDH	c	c	c	c	c	c	c	c	d	b	a	c	c
GPI	c	c	c	c	c (0.833) d (0.167)	b (0.167) c (0.833)	c	c	a (0.50) c (0.50)	c	e	c	c
LA	b	b	b	b	b	b	b	b	b	b	b	b	a
PEP-B	f	f	g	f	d (0.333) f (0.667)	f	c (0.50) e (0.50)	c	f	e	a	b	a
MPI	e	e (0.833) f (0.167)	e	e	e	c (0.167) e (0.833)	c	c	b (0.50) c (0.50)	e	a	d	e
CK1	b	b	b	b	b	b	b	b	b	b	a	a	a
CK2	a	a	a	a	a	a	a	a	a	a	a	a	b
G3PDH	b (0.90) c (0.10)	b	b	b	a (0.167) b (0.833)	b (0.833) c (0.167)	b	b	b (0.50) c (0.50)	b	c	b	d
ACOH1	c	c	c	c	a (0.333) c (0.667)	a	c	c	c	c	c	b	c
ACOH2	a	a	a	a	a	a	b	b	b	b	b	b	b
SDH	d	d	d	c (0.667) d (0.333)	d	d	d	d	d	d	b	d	a
PGM2	c	c	c	c	b (0.333) c (0.667)	b	d	d	d	c	c	a	c

TABLE 2
CONTINUED

	LEUEC	LEUDA	LEUCR	LEUNA	LEUEY	LEUNN	SALSA	SALPA	LUNUL	RUFIG	PALBI	RMELA	MFORT
ADA	a (0.30) b (0.40) d (0.30)	b (0.50) d (0.50)	d	b (0.333) d (0.50) e (0.167)	b (0.167) d (0.50) e (0.167) f (0.167)	b (0.333) d (0.667)	d	c (0.50) d (0.50)	d	d	e	d	g
MDHP1	c	c	c	c	c	c	a	b (0.50) c (0.50)	c	c	d	c	c
MDHP2	b	b	b	b	b	a (0.667) b (0.333)	c	c	b	b	b	b	b
PEP-D	b	b	b	b (0.333) e (0.667)	a (0.333) b (0.333) c (0.334)	b (0.333) c (0.667)	h	c (0.25) h (0.75)	d	b	b	g	f

[a] Acronyms for taxa are in Table 1 and in the text. Abbreviations for loci can be found in Murphy et al. (1990). The following loci were monomorphic and fixed for the same allele in all taxa: MDH1, MDH2, AAT2, ?DH, SOD1, SOD2, LDHA, LDHB, G6PDH, AK, GDA, ADH, PGM1, GTDH, ESTD, EAP, AB, FUMH. ?DH is an unknown dehydrogenase. AB is a general protein.

TABLE 3

GENETIC DISTANCES (NEI 1978, BELOW DIAGONAL; ROGERS 1972, ABOVE DIAGONAL) FOR TAXA ANALYZED IN THIS STUDY[3]

	LEUEC	LEUDA	LEUCR	LEUNA	LEUEY	LEUNN	SALSA	SALPA	LUNUL	RUFIG	PALBI	RMELA	MFORT
LEUEC	—	0.014	0.046	0.046	0.069	0.137	0.205	0.190	0.199	0.127	0.263	0.208	0.264
LEUDA	0.001	—	0.045	0.045	0.073	0.135	0.197	0.185	0.197	0.126	0.265	0.201	0.271
LEUCR	0.037	0.033	—	0.075	0.087	0.167	0.186	0.187	0.213	0.108	0.270	0.189	0.270
LEUNA	0.022	0.020	0.055	—	0.083	0.153	0.212	0.199	0.212	0.156	0.278	0.216	0.259
LEUEY	0.014	0.013	0.036	0.023	—	0.110	0.212	0.197	0.212	0.168	0.298	0.204	0.287
LEUNN	0.114	0.111	0.146	0.125	0.047	—	0.247	0.234	0.254	0.248	0.376	0.247	0.370
SALSA	0.215	0.205	0.201	0.215	0.189	0.251	—	0.057	0.199	0.203	0.321	0.213	0.348
SALPA	0.187	0.180	0.184	0.190	0.161	0.223	0.028	—	0.200	0.214	0.314	0.214	0.332
LUNUL	0.178	0.171	0.201	0.182	0.161	0.236	0.175	0.159	—	0.186	0.304	0.240	0.358
RUFIG	0.126	0.122	0.114	0.147	0.130	0.248	0.217	0.218	0.167	—	0.270	0.216	0.297
PALBI	0.299	0.302	0.315	0.309	0.309	0.446	0.383	0.367	0.330	0.315	—	0.297	0.297
RMELA	0.224	0.214	0.210	0.224	0.186	0.254	0.235	0.218	0.236	0.244	0.353	—	0.297
MFORT	0.302	0.308	0.315	0.290	0.296	0.439	0.424	0.387	0.412	0.353	0.353	0.353	—

[a] Acronyms for taxa can be found in Table 1.

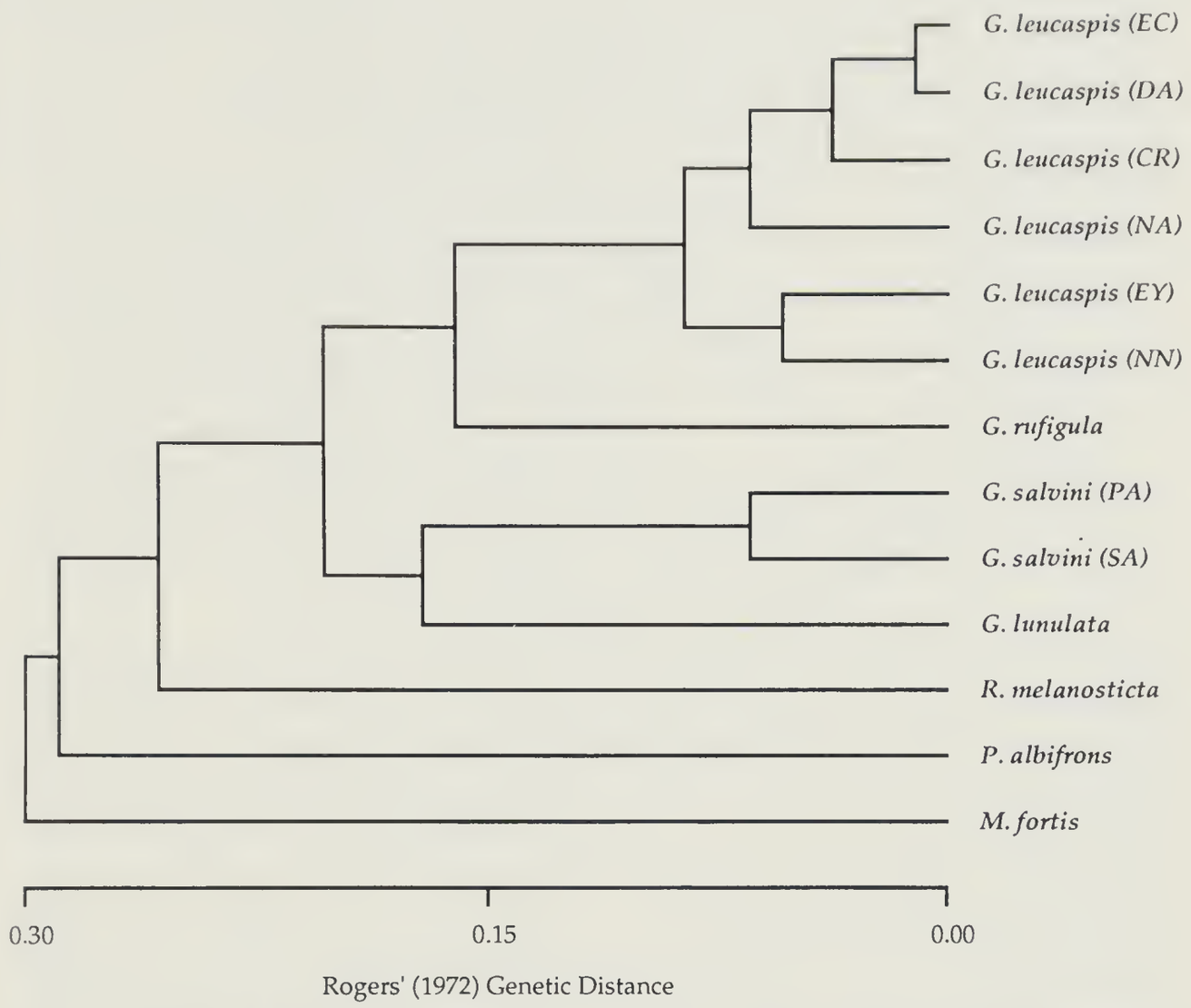

FIG. 2. UPGMA phenogram of Rogers' (1972) genetic distance (Table 3) for *Gymnopithys* species and population samples. The cophenetic correlation coefficient for the phenogram is 0.94. "FITCH" and "KITSCH" trees (see text) have the same topology. The two letter codes after the species name reference the last two letters of the acronyms found in Table 1.

populations of *G. leucaspis* and *G. salvini*. These data also demonstrate a high degree of population subdivision among the majority of Neotropical forest species analyzed to date.

Gymnopithys antbirds are obligate ant-following birds, which could result in increased movements as they search for the ant swarms at which they forage. This life-history characteristic has the possible genetic consequence of increased gene flow, which would lead to the prediction that genetic subdivision (i.e., F_{st} or genetic distances) within *Gymnopithys* species should be low relative to other more sedentary forest birds that forage for insects on individual territories. This prediction is not supported by the genetic data, which indicate that *Gymnopithys* separated by even small geographic distances are genetically differentiated. LEUNN and LEUEY are separated by approximately 100 km (and no major rivers) and their genetic distance is 0.047, which is equivalent to the genetic

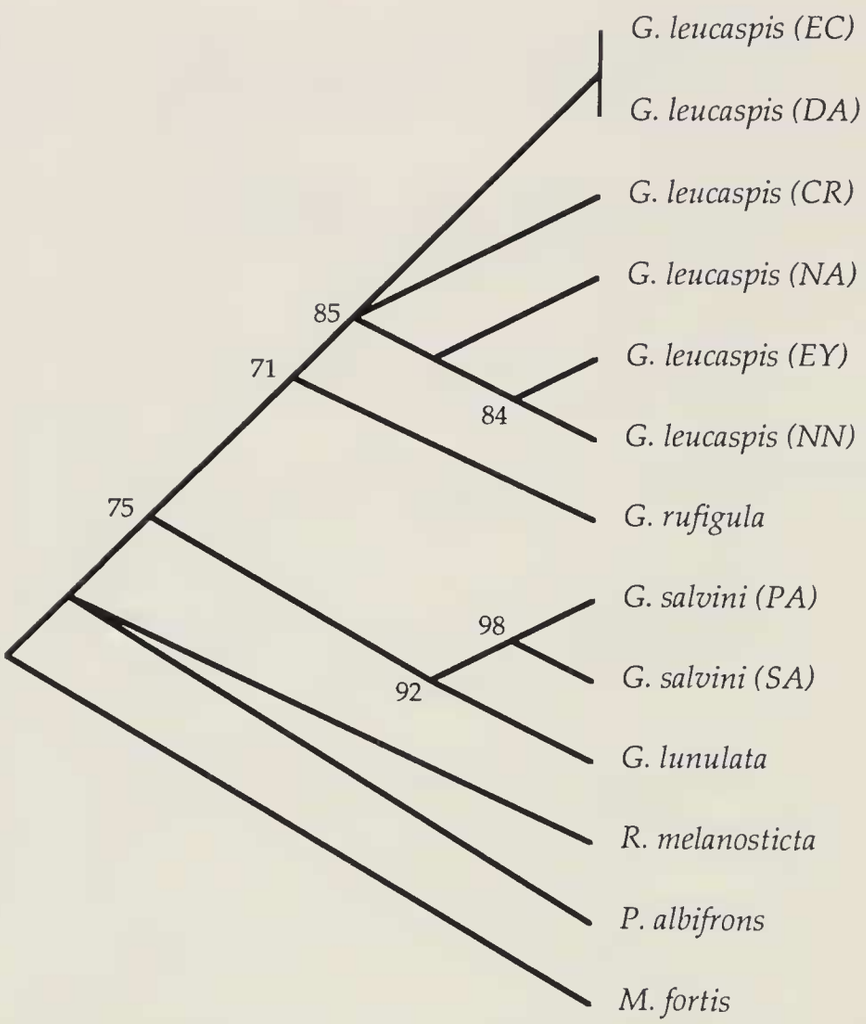

FIG. 3. Cladistic assessment of allelic variability (see text) for *Gymnopithys* species and population samples. The two letter codes after the species name reference the last two letters of the acronyms found in Table 1.

distances separating many species of *Dendroica* warblers (Barrowclough and Corbin 1978).

The genetic data support the monophyly of the genus *Gymnopithys* relative to three other genera of ant-following formicariids. To address behavioral evolution within the Formicariidae, the next step is to document whether the ant-following formicariids are indeed each other's closest relatives. If so, this would indicate that a complex life-history strategy and associated behaviors are key innovations that evolved once in the history of antbirds, and thus document monophyly of a group of antbird genera. Hackett and Rosenberg (1990) documented a similar situation in *Myrmotherula* antwrens; the presence of a particular behavioral, life-history character (dead-leaf foraging) paralleled allozymic results in defining a lineage of antbirds.

The genetic data support a sister-taxon relationship between *Gymnopithys lunulata* and *G. salvini*. I recommend, therefore, that these species be placed next to each other in linear classifications. There is weak support

TABLE 4
F_{ST} VALUES FOR NEOTROPICAL FOREST TAXA[a]

Species	F_{st} (SE)
Wedge-billed Woodcreeper (*Glyphorynchus spirurus*)	0.232 (0.140)
White-cheeked Antbird (*Gymnopithys leucaspis*)	0.365 (0.099)
White-throated Antbird (*G. salvini*)	0.333 (0.097)
Black-faced Antbird (*Myrmoborus myotherinus*)	0.170 (0.063)
White-plumed Antbird (*Pithys albifrons*)	0.037 (0.012)
Blue-crowned Manakin (*Pipra coronata*)	0.125 (0.064)
Golden-headed Manakin (*P. erythrocephala*)[b]	0.235 (0.127)
Blue-backed Manakin (*Chiroxiphia pareola*)	0.194 (0.042)

[a] F_{st} for non-*Gymnopithys* species were calculated from allele frequency data of Capparella (1987).
[b] Includes *P. rubrocapilla*, the allospecies of *P. erythrocephala* from south of the Amazon river.

for considering the populations of *G. leucaspis* in Central America and South America west of the Andes as distinct (*G. bicolor*), and I recommend study with more sensitive molecular markers. Willis (1967) hypothesized a close relationship between *G. leucaspis, G. bicolor,* and *G. rufigula,* based on vocalizations, and suggested that they should be placed in the same species. Although genetic data weakly support a sister-taxon relationship between *G. rufigula* and *G. leucaspis,* each is diagnosable by a number of allozymic and plumage characters. Therefore, considering *G. rufigula* and *G. leucaspis* as conspecific is not recommended.

Biogeography.—One proposed advantage of molecular data is that genetic differences between taxa accrue in an approximately time-dependent manner (Wilson et al. 1977); therefore, a molecular clock can be calibrated and the age of splitting events can be estimated. The potential to date approximate splitting events using molecular clocks has not been widely explored (see Murphy 1983, Cadle 1985, Zink 1988, and Zink and Avise 1990 for some examples). In addition, the concept of molecular clocks is controversial, and a variety of molecular clocks have been proposed for avian taxa (Gutiérrez et al. 1983, Marten and Johnson 1986, Sibley et al. 1988). Two calibrations for allozyme data estimate that one unit of Nei's (1978) genetic distance corresponds to 19–26 million years of independent evolution (Gutiérrez et al. 1983, Marten and Johnson 1986). For *Gymnopithys,* these calibrations suggest that the genus has been evolving independently for approximately six million years. The species seem to be old as well; origin of *G. lunulata, G. salvini, G. leucaspis,* and *G. rufigula* may have occurred three to five million years ago. Because the ranges of *Gymnopithys* species are delimited by rivers (Fig. 1), I hypothesize that the development of major river systems in South America (Capparella

1987, 1988, 1991) separated a formerly widespread range of the ancestral *Gymnopithys* roughly three to six million years ago. Within *Gymnopithys leucaspis* and *salvini,* divergence of populations seemed to have occurred early in the Pleistocene (700,000 to 1,000,000 years ago), perhaps as a result of the effects of glacial periods on the distribution of Neotropical forests (Haffer 1974).

Because *Gymnopithys leucaspis* is distributed in both South and Central America, relationships among its populations may shed light on hypotheses concerning the origin of Central American lowland birds. The landbridge connection between southern Central America and South America was completed three to five million years ago (Malfait and Dinkleman 1972, Pindell and Dewey 1982). One hypothesis explaining the distribution of some Central American lowland taxa is that South American taxa dispersed to the Central American landmass after the landbridge was completed (Haffer 1967, 1974, 1985, 1987; Cracraft 1985; Cracraft and Prum 1988) and that Pleistocene climatic fluctuations subsequently effected the separation of Central American and South American lowland forests (Haffer 1974, 1987). The genetic data suggest that *G. leucaspis* was present in South America when the landbridge connection was formed. The pattern of genetic distances (Fig. 2) suggests that Central American and Ecuadorian populations form a group (although the cladistic analysis of allozyme data was unable to recover this) and that separation of Costa Rican (LEUCR) from Ecuadorian (LEUEC) populations occurred 700,000–900,000 years ago. This supports the hypotheses of Haffer (1967, 1974, 1985, 1987), Cracraft (1985), and Cracraft and Prum (1988) that Central American taxa would be most closely related to taxa found in Ecuador, in the Chocó region of western South America, and that divergence occurred after the landbridge was completed (some time during the Pleistocene).

ACKNOWLEDGMENTS

This research was supported by grants from the Fugler Fellowship of the Louisiana State Univ. Museum of Natural Science, the Chapman Fund of the American Museum of Natural History, the American Ornithologists' Union, National Sigma Xi, and the National Science Foundation (NSF Doctoral Dissertation Improvement Grant, BSR-9101289). I am grateful to J. M. Bates, K. J. Burns, A. P. Capparella, R. Chapman, J. Cracraft, M. Hafner, D. Pashley, J. V. Remsen, K. V. Rosenberg, and R. M. Zink for helpful comments on this manuscript. Also, I wish to thank the many institutions and governmental agencies for their assistance in obtaining specimens used in this study.

LITERATURE CITED

ARCHIE, J. W. 1989a. A randomization test for phylogenetic information in systematic data. Syst. Zool. 38:239–252.

———. 1989b. Homoplasy excess ratios: new indices for measuring levels of homoplasy in phylogenetic systematics and a critique of the consistency index. Syst. Zool. 38:253–269.

———, C. Simon, and A. Martin. 1989. Small sample size does decreasc thc stability of dendrograms calculated from allozyme-frcquency data. Evolution 43:678–683.

Avise, J. C. and C. F. Aquadro. 1982. A comparative study of genetic distances in the vertebrates. Pp. 151–185 *in* Evolutionary biology, vol. 15 (M. K. Hecht, B. Wallace, and G. T. Prance, eds.). Plenum Press, New York, Ncw York.

Barrowclough, G. F. and K. W. Corbin 1978. Genetic variation and differentiation in the Parulidae. Auk 95:691–702.

——— and N. K. Johnson. 1988. Genetic structure of North American birds. Proc. Int. Ornithol. Congr. 19:1630–1638.

Buth, D. G. 1984. The application of electrophoretic data in systematic studies. Ann. Rev. Ecol. Syst. 15:501–522.

Cadle, J. E. 1985. The Neotropical colubrid snake fauna (Serpentes: Colubridae): lineage components and biogeography. Syst. Zool. 34:1–20.

Capparella, A. P. 1987. Effects of riverine barriers on genetic differentiation of Amazonian forest undergrowth birds. Ph.D. diss., Louisiana State Univ., Baton Rouge, Louisiana.

———. 1988. Genetic variation in Neotropical birds: implications for the speciation process. Proc. Int. Ornithol. Congr. 19:1658–1664.

———. 1991. Neotropical avian diversity and riverine barriers. Proc. Int. Ornithol. Congr. 20:307–316.

Cracraft, J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Ornithol. Monogr. 36:49–84.

——— and R. O. Prum. 1988. Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. Evolution 42:603–620.

Farris, J. S. 1972. Estimating phylogenetic trees from distance matrices. Am. Nat. 106: 645–668.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 79:783–791.

———. 1986. PHYLIP-Phylogeny inference package, Version 3.0. Univ. Washington, Dept. of Genetics, Seattle, Washington.

Gerwin, J. A. and R. M. Zink. 1989. Phylogenetic patterns in the genus *Heliodoxa* (Aves: Trochilidae): an allozymic perspective. Wilson Bull. 101:525–542.

Gill, F. B. and J. A. Gerwin. 1989. Protein relationships among hermit hummingbirds. Proc. Acad. Nat. Sci. Philadelphia 141:409–421.

Gorman, G. C. and J. Renzi, Jr. 1979. Genetic distance and heterozygosity estimates in electrophoretic studies: effects of sample size. Copeia 1979:242–249.

Gutiérrez, R. J., R. M. Zink, and S. Y. Yang. 1983. Genic variation, systematic, and biogeographic relationships of some galliform birds. Auk 100:33–47.

Hackett, S. J. 1989. Effects of varied electrophorctic conditions on dctection of evolutionary patterns in the Laridae. Condor 91:73–90.

——— and K. V. Rosenberg. 1990. Evolution of South Amcrican antwrens (Formicariidae): comparison of phenotypic and genctic diffcrentiation. Auk 107:473–489.

Haffer, J. 1967. Speciation in Colombian forest birds west of the Andes. Amcr. Mus. Novitates 294:1–57.

———. 1974. Avian speciation in tropical South America. Publ. Nuttall Ornithol. Club 14.

———. 1985. Avian zoogeography of the Neotropical lowlands. Ornithol. Monogr. 36: 113–146.

———. 1987. Biogeography of Neotropical birds. Pp. 105–150 *in* Biogeography and quaternary history in tropical America (T. C. Whitmore and G. T. Prance, eds.). Clarendon Press, Oxford, England.

Kluge, A. G. and J. S. Farris. 1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18:1–32.

Malfait, B. J. and M. G. Dinkleman. 1972. Circum-Caribbean tectonic and igneous activity and the evolution of the Caribbean plate. Geol. Soc. Am. Bull. 83:251–272.

Marten, J. A. and N. K. Johnson. 1986. Genetic relationships of North American cardueline finches. Condor 88:409–420.

Meyer de Schauensee, R. 1966. The species of birds of South America with their distribution. Livingston Publ. Co., Narberth, Pennsylvania.

Mickevich, M. M. and C. M. Mitter. 1981. Treating polymorphic characters in systematics: a phylogenetic treatment of electrophoretic data. Pp. 45–58 *in* Advances in cladistics, vol. 1 (V. A. Funk and D. R. Brooks, eds.). New York Botanical Gardens, New York, New York.

Murphy, R. W. 1983. Paleobiogeography and genetic differentiation of the Baja California herpetofauna. Occas. Pap. Calif. Acad. Sciences 137:1–48.

———, J. W. Sites, Jr., D. G. Buth, and C. H. Haufler. 1990. Proteins 1: isozyme electrophoresis. Pp. 45–126 *in* Molecular systematics (D. M. Hillis and C. Moritz, eds.). Sinauer Assoc., Inc., Sunderland, Massachusetts.

Nei, M. 1978. Estimation of average heterozygosities and genetic distance from a small number of individuals. Genetics 89:583–590.

Pindell, J. and J. F. Dewey. 1982. Permo-Triassic reconstruction of Western Pangea and the evolution of the Gulf of Mexico/Caribbean region. Tectonics 1:179–211.

Rogers, J. S. 1972. Measures of genetic similarity and genetic distance. Studies in genetics VII. Univ. Texas Publ. No. 7213:145–153.

——— and R. C. Cashner. 1987. Genetic variation, divergence, and relationships in the subgenus *Xenisma* of the genus *Fundulus*. Pp. 251–264 *in* Community and evolutionary ecology of North American stream fishes (W. J. Matthews and D. C. Heins, eds.). Univ. Oklahoma Press, Norman, Oklahoma.

Sanderson, M. J. 1989. Confidence limits on phylogenies: the bootstrap revisited. Cladistics 5:113–130.

Sibley, C. G., J. E. Ahlquist, and B. L. Munroe. 1988. A classification of the living birds of the world based on DNA-DNA hybridization studies. Auk 105:409–423.

Swofford, D. L. 1981. On the utility of the distance Wagner procedure. Pp. 25–43 *in* Advances in cladistics, vol. 1 (V. A. Funk and D. R. Brooks, eds.). New York Botanical Gardens, New York, New York.

———. 1990. PAUP: phylogenetic analysis using parsimony, Version 3.0. Illinois Natural History Survey, Champaign, Illinois.

——— and S. H. Berlocher. 1987. Inferring evolutionary trees from gene frequency data under the principle of maximum parsimony. Syst. Zool. 36:293–325.

——— and R. B. Selander. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72:281–283.

Willis, E. O. 1967. The behavior of bicolored antbirds. Univ. Calif. Publ. Zool. 79:1–132.

———. 1968. Studies of the behavior of Lunulated and Salvin's antbirds. Condor 70:128–148.

Wilson, A. C., S. S. Carlson, and T. J. White. 1977. Biochemical evolution. Ann. Rev. Biochem. 46:573–639.

WRIGHT, S. 1978. Evolution and genetics of populations. Vol. 4, Variability within and among populations. Univ. Chicago Press, Chicago, Illinois.

ZIMMER, J. T. 1937. Studies of Peruvian birds. No. XXV. Notes on the genera *Thamnophilus, Thamnocharis, Gymnopithys,* and *Ramphocaenus.* Amer. Mus. Novitates 917: 1–16.

ZINK, R. M. 1988. Evolution of Brown Towhees: allozymes, morphometrics and species limits. Condor 90:72–82.

——— AND J. C. AVISE. 1990. Patterns of mitochondrial DNA and allozyme evolution in the avian genus *Ammodramus.* Syst. Zool. 39:148–161.